

Hindlimb Suspension and Hind Foot Reversal in *Varecia variegata* and Other Arboreal Mammals

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ABSTRACT The foot, perhaps more than any other region of the primate body, reflects the interaction of positional behaviors with the geometric properties of available supports. The ability to reverse the hind foot during hindlimb suspension while hanging from a horizontal support or descending a large diameter vertical trunk has been noted in many arboreal mammals, including primates. Observations of *Varecia variegata* in the wild and under seminatural conditions document hindlimb suspension in this lemurid primate. The kinematics and skeletal correlates of this behavior are examined. Analogy is made with the form and function exhibited by nonprimate mammalian taxa employing this behavior. Examples of carnivores and rodents display very similar adaptations of the tarsals while other mammals, such as the xenarthrans, accomplish a similar end by means of different morphologies. However, a suite of features is identified that is shared by mammals capable of hind foot reversal. Hindlimb suspension effectively increases the potential feeding space available to a foraging mammal and represents a significant, and often unrecognized, alternative adaptive strategy to forelimb suspension and prehensile-tail suspension in primates. *Am J Phys Anthropol* 103:85–102, 1997. © 1997 Wiley-Liss, Inc.

Grand's (1972) mechanical interpretation of terminal branch feeding drew attention to the significance of the adaptive strategy of forelimb suspensory feeding and locomotion. The elongated mobile arms of the gibbon, for example, permit more economy of movement and exploitation of an increased feeding space, encompassing the space both above and below the support, while a more generalized arboreal quadrupedal monkey is generally restricted to the above-branch space. Mittermeier and Fleagle (1976) drew further attention to the importance of suspended postures as a feeding adaptation in the spider monkey. They noted that by hanging from its prehensile tail, a spider mon-

key's potential area of movement for feeding is increased even more than by arm suspension alone.

We note and examine an alternative adaptive strategy for increased exploitation of feeding space that has received surprisingly little attention in primate field studies—the ability of some primates to reverse the foot

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during hindlimb suspension from a horizontal support or headfirst descent on a large diameter vertical support. This behavior occurs frequently in a number of prosimian and anthropoid primates, including *Nycticebus* (Jenkins and McClearn, 1984), *Otolemur* (Bishop, 1964), *Varecia* (Dagosto and Meldrum, personal observation), *Propithecus*, *Daubentonia*, *Eulemur*, *Chiropotes* (van Roosmalen et al., 1981; Kinzey, personal communication; personal observation), *Cacajao* (Eimerl and DeVore, 1965; Walker, personal communication), *Pithecia* (Meldrum, personal observation), *Saguinus* (Garber, personal communication), and *Cercopithecus* (Meldrum, personal observation).

Hindlimb suspension has received more attention in a number of climbing nonprimate mammals, including various marsupials, sciurids, procyonids, viverrids, tupaiids, and felids (Leyhausen, 1963; Trapp, 1972; Cartmill, 1974; Jenkins and McClearn, 1984; McClearn, 1992). It has also been inferred for some extinct mammals as well (Jenkins and Krause, 1983; Gingerich and Gunnell, 1989). This behavior involves extreme plantarflexion and supination of the ankle such that the plantar surface of the foot is facing nearly anteriorly. Jenkins and McClearn (1984) identified a number of skeletal features associated with increased range of motion at the astragalocuboid, subastragalar, and transverse tarsal joints. These included shortened tibial malleolus, long astragalar trochlea (subtending an arc of 180 degrees), oblique astragalar crest, angled posterior calcaneal facet, bulbous mediolaterally broad astragalar head, and crescent-shaped calcaneocuboid facet. A number of these features have also been observed in the foot skeleton of the bearded saki monkey, *Chiropotes* (Fleagle and Meldrum, 1988). It was suggested that these similarities in ankle structure were related to *Chiropotes*' habit of hindlimb suspension as reported anecdotally by Mittermeier (1977) and van Roosmalen et al. (1981). Walker and Ayres (1996) and Ayres (1986) have since documented the high frequency with which both *Chiropotes* and *Cacajao* employ hindlimb suspensory postures when feeding and displaying.

In this paper, we describe the role of hindlimb suspension in the prosimian pri-

mate, *Varecia variegata*. The frequency and context of this behavior were observed in the wild by Dagosto. Meldrum describes the kinematics of this postural behavior observed in *Varecia* under seminatural conditions, and provides a radiographic assessment of the bone-joint relationships. White compares and contrasts skeletal correlates of this behavior with nonprimate mammalian analogs. Finally, we discuss the common morphological features and adaptive significance of this behavior.

MATERIALS AND METHODS

The positional behavior of *Varecia variegata* was studied at Ranomafana National Park, located in southeastern Madagascar at 47°E, 21°S (Dagosto, 1994, 1995). Data were collected during two field seasons: June–August 1990 and March–May 1991. Focal animals were followed during daylight hours. Positional behavior was recorded in two ways: by continuous recording using the "bout" method (Fleagle, 1976) and by instantaneous time samples recorded at 2-minute intervals. The results presented here are based on 121 hours of observation of two adult individuals of each species, which resulted in 2,137 bouts and 2,264 time samples of postures.

Visual observations and photographic and video recordings were made of several species of prosimians housed at the Duke Primate Center under seminatural conditions. These included *Varecia variegata*, *Eulemur macaco*, *E. fulvus*, *E. rubriventer*, and *Propithecus verreauxi*. The specimens were maintained in a variety of enclosures including a large fenced area of forest (appr. 2 ha) and an outdoor, silo-shaped, wire enclosure (approximately 5 m high and 3.5 m across). Cages were equipped with a variety of vertical, horizontal, and inclined supports of various diameters. The primates were quite habituated to the presence of humans, thus allowing observations and filming to be carried out inside the enclosures and cages in very close proximity to the subjects. On occasion the subjects were coaxed into a suspensory posture with a food reward.

Radiographs were taken of a fresh cadaver of an adult female *Varecia variegata* (DPC 1186). The hindlimbs were

TABLE 1. Percentage of use of postures by bouts and time samples

	<i>Varecia variegata</i>		<i>Lemur fulvus</i>		<i>Lemur rubriventer</i>		<i>Propithecus diadema</i>	
	Bouts ¹	TS ²	Bouts	TS	Bouts	TS	Bouts	TS
Lie	1.5	5.5	0.6	9.3	0.9	8.7	0.6	0.7
Sit	48.0	82.5	69.3	85.5	50.9	79.6	44.6	78.3
Stand	30.5	7.5	19.1	3.6	28.8	8.0	1.5	0.3
Suspend	17.0	4.2	0.8	0.1	0.9	0.1	6.5	2.7
Vertical cling	2.0	0.4	10.8	1.5	18.4	3.6	46.9	17.9

¹ Bouts, continuous sampling (Fleagle, 1976).² Time samples (TS), instantaneous samples at 2-minute intervals.

TABLE 2. Percentage of types of suspensory postures

	<i>Varecia variegata</i>		<i>Lemur fulvus</i>		<i>Lemur rubriventer</i>		<i>Propithecus diadema</i>	
	Overall	Feeding	Overall	Feeding	Overall	Feeding	Overall	Feeding
Quadrupedal	50	50	25	100	9	0	18	16
Bipedal	39	38	60	0	48	41	27	11
Tripedal	10	11	5	0	0	0	42	58
Bimanual	1	1	10	0	43	59	13	15

positioned to approximate the postures of living specimens as recorded photographically or from video stills. The limbs were secured in position by taping them to a ready-pac x-ray film cassette. While this method clearly has its limitations and is not intended to precisely reproduce the skeletal relationships of a living foot, it nevertheless provides an opportunity to reasonably approximate the relative positions and relationships of the tarsal elements, and augments the functional analysis of skeletal morphology.

Observations of skeletal morphology were made on dry, disarticulated skeletons of selected specimens in the collections of the Duke Primate Center and the National Museum of Natural History.

RESULTS

Field observations

Whether measured by frequency (proportion of bouts) or by time spent (proportion of time samples), wild *Varecia variegata* engages in suspensory postures much more often than the other two species of lemur (*Eulemur fulvus rufus* and *Eulemur rubriventer*) or the indriid (*Propithecus diadema*) which were studied concurrently (Dagosto, 1994). Considering all postural bouts, the frequency of suspensory postures in *Varecia* is 17% compared to less than 1.0% in the two lemurs and 6.5% in *Propithecus*

(Table 1). The time spent in suspensory postures is 4.0% in *Varecia* vs. 0.1% or less in lemurs and 2.7% in *Propithecus* (Table 1). The difference in use of suspensory postures in *Varecia* compared to any of these other Malagasy lemurs is statistically significant (Dagosto, 1994). Despite the fact that suspensory postures were frequently used by *Varecia*, this species, like the other lemurs, only rarely moved in an nonpronograde attitude.

In *Varecia*, quadrupedal suspension is the most commonly adopted suspensory posture, followed by bipedal and tripedal (two feet and one hand) stances (Table 2). Bimanual suspension is rare. Although isolated instances of quadrupedal suspensory postures occur, quadrupedal postures are more frequent partly because they are also end points in a full bipedal suspensory event. Tripedal postures are likewise adopted as transitional phases between quadrupedal and bipedal suspension, but also independently as when reaching for a food item with one hand while the other hand remains on the support. Recovery from suspensory postures is most often accomplished by "flipping" back up from a quadrupedal suspensory posture or less commonly by dropping to the branch below.

In contrast to *Varecia*, in the other species bipedal and tripedal postures are more common than quadrupedal suspension (Table 2). In these species, the "quadrupedal phase" of

TABLE 3. Percentage of suspensory postures derived from feeding

	<i>Varecia variegata</i>	<i>Lemur fulvus</i>	<i>Lemur rubriventer</i>	<i>Propithecus diadema</i>
Quadrupedal	90	60	0	39
Bipedal	89	0	64	19
Tripedal	100	0	0	62
Bimanual	100	0	100	52
Total	91	15	74	45

TABLE 4. Postures used during feeding (bouts)

	<i>Varecia variegata</i>	<i>Lemur fulvus</i>	<i>Lemur rubriventer</i>	<i>Propithecus diadema</i>
Lie	6.50	0.13	0.10	0.75
Sit	33.00	63.89	44.05	52.07
Stand	32.50	24.42	36.56	3.03
Suspend	26.00	0.93	0.83	8.97
Vertical cling	0.50	10.76	18.44	35.16

a bipedal or tripedal suspensory event was of rapid transitional nature and of a short enough duration (<1 second) that it was not recorded as a separate posture.

Virtually all suspensory postures in *Varecia* occur during feeding and foraging (Table 3). This is less true in the other species where suspensory postures also occur in other contexts, particularly in play and grooming. If one looks at postures adopted during feeding/foraging (Table 4) it is again clear that *Varecia* adopts suspensory postures far more often than any of the other species.

In *Varecia*, suspensory postures are adopted almost exclusively in the canopy or terminal branch areas of large fruit trees (Table 5). The supports used during suspensory events are overwhelmingly small (<7.5 cm diameter; the majority are ≤ 2.5 cm). Often more than one of these small supports was grasped during suspension. Horizontal supports are most frequently chosen, but oblique supports are also well represented. The supports used during suspensory postures are usually flexible enough to deform under the animal's weight.

Kinematics

The seminatural setting of the Duke Primate Center provided an opportunity to study the kinematics of hindlimb suspension and related positional behaviors that

are usually impossible to observe and record in the wild. Of all of the prosimians observed, *Varecia* most readily assumed a bipedal suspensory posture, requiring no initial coaxing by food reward. This posture was employed in a variety of contexts—foraging, grooming, play, investigating observers and their photographic equipment, or by a solitary individual for no apparent objective. The descriptions offered here are specifically for postures assumed by *Varecia*, but are applicable to other prosimian taxa, such as *Propithecus verreauxi* and *Eulemur macaco*. While *Eulemur fulvus* would adopt a hindlimb suspensory posture, it never achieved the full extent of plantar flexion seen in *Varecia*, *Propithecus*, and *Eulemur macaco*, and tripedal suspensory postures were clearly preferred. Interestingly, no amount of coaxing with food rewards could illicit a hindlimb suspensory posture from *E. rubriventer*. This agrees with Tilden's (1990) observation of very low incidence of suspensory behavior by captive *E. rubriventer*.

Hindlimb suspension in nonclawed species with grasping digits can be divided into two postures, which we will designate "opposed grip" and "parallel grip" (Fig. 1). An opposed grip is defined as hindlimb, or bipedal suspension, where the plantar surfaces of the feet are applied to opposite sides of a relatively horizontal support (Fig. 1A). A parallel grip is defined as bipedal suspension where the plantar surfaces of the feet are applied to the same side of a relatively horizontal support (Fig. 1B). The context and kinematics of each of these grips and associated positional behaviors differ somewhat and are dealt with separately.

The opposed grip requires less reversal of the foot and is frequently assumed from a quadrupedal suspensory posture, from which point the forelimbs simply release their grasp and the hindlimbs and vertebral column are extended. From an above-branch quadrupedal position the kinematic sequence is as follows. The individual's body is typically oriented in line with the support. It lunges to one side of the support releasing one or both hands. If only one hand is released, the contralateral hand (i.e., hand opposite the direction of the lunge) briefly maintains its grasp. Simultaneously, the contralateral foot

TABLE 5. Percentage of suspensory postures by *Varecia variegata* in arboreal contexts

Tree location		Substrate orientation		Substrate size	
Crown	89.0	Horizontal	56.1	Tiny (<2.5 cm)	55.1
Major branch	10.6	Oblique	43.6	Small (2.5–7.5 cm)	44.1
Trunk	0.0	Vertical	0.4	Medium (10–15 cm)	0.8
Liana	0.3				



Fig. 1. Hindlimb suspension displayed by two captive ruffed lemurs (*Varecia variegata*) exhibiting the opposed grip (A) and the parallel grip (B).

maintains a loose grasp of the support, while sliding across the superior surface of the support until it reaches the opposite side. The ipsilateral foot releases its grip and passes inferior to the support to reestablish a grasp on the other side of the support.

The parallel grip is usually assumed from a position in which the body is perched across or perpendicular to the support. Initially the feet are in an opposed grip, then the grip of the ipsilateral foot (the foot on the side of the support toward which the primate is facing) is released and externally rotated so that the lateral digits are facing

posteriorly. The primate then releases hand grips and dives forward, to the side of the horizontal support. The pedal digits slide over to the superior surface of the support, while the halluces are situated on the inferior surface. Very frequently, particularly on relatively narrow (ca. 5 cm) but stable supports, the suspensory posture is maintained by a hooklike posture with principal contact at the middle and distal phalanges of the lateral digits, while the hallux makes no contact with the substrate and is simply flexed across the volar surface of the foot.

Radiography

Radiographs of the fresh foot and ankle of a *Varecia*, positioned to approximate the postures observed in the living specimens, provide a noninvasive method of visualizing the configuration of the tarsal elements during various suspensory activities. Hindfoot reversal involves the combination of extreme astragalocrural plantarflexion, subastragalar inversion, and transverse tarsal supination.

Tracings from radiographs (Figs. 2 and 3) reveal extreme plantarflexion of the astragalocrural, or upper ankle, joint. The tibial trochlear surface contacts the most proximal aspect of the astragalar trochlea. This is most extreme in the parallel grip, especially when the hooklike posture is employed without the assistance of the hallux. In this case the cruropedal angle approaches 180 degrees. The presence of a distinct contact facet on the posterior surface of the distal fibula in some skeletal specimens suggests that the calcaneal tuberosity actually contacts or closely approximates the fibula. Extreme inversion is evident at the subtalar joint. The posterior calcaneal facet of the talus is riding quite proximally on the posterior talar facet of the calcaneus. Supination occurs at the transverse tarsal joint complex. The calcaneocuboid and astragala-

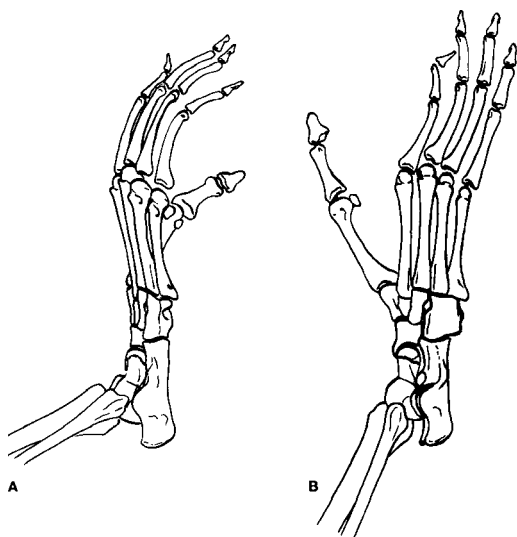


Fig. 2. Tracing of a radiograph of the foot and ankle skeleton of *Varecia variegata* in a neutral position (A) and positioned to approximate an opposed grip (B).

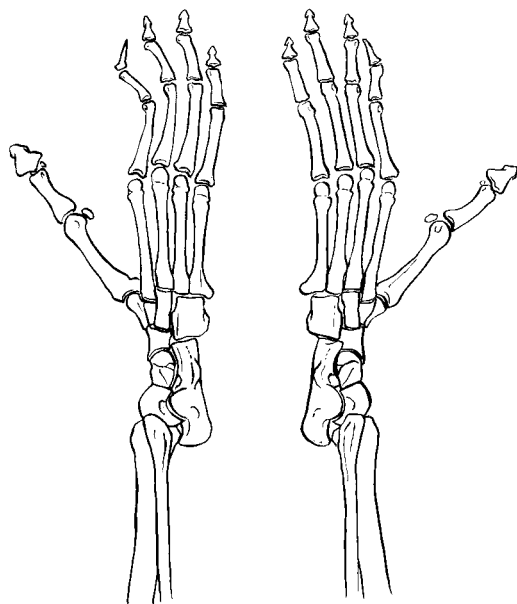


Fig. 3. Tracing of a radiograph of the foot and ankle skeleton of *Varecia variegata* positioned to approximate a parallel grip.

vicular joints are rotated externally. This movement exposes the superolateral aspect of the spherical astragalar head. Although these radiographs represent cadaveric mate-

rial, overall similarity of the skeletal associations observed in published radiographs of living specimens of other living mammal specimens is noted (e.g. Jenkins and McClearn, 1984).

Skeletal morphology

Skeletal adaptations for foot reversal and hindlimb suspension are evident in *Varecia*. The tibial malleolus has a rounded projection that corresponds to a concave medial facet on the astragalus (Fig. 4A). The distal articular surface on the tibia is not distinctly divided and is triangular; the medial side is longer and more concave. This morphology reflects the narrow and anteroposteriorly elongated astragalar trochlea, which spans 180 degrees (Fig. 5A). This arrangement permits a great degree of anteroposterior movement at the ankle joint, evidenced by a facet on the posterior fibula that contacts the tuberosity of the calcaneus in extreme plantar flexion. The medial articular surface of the trochlea is both higher and longer than the lateral; asymmetry causes the axis of rotation to be somewhat oblique, a feature common to many mammals that invert in plantar flexion and evert in dorsiflexion. The astragalar head is mediolaterally broad and bulbous and the neck is long and angled medially (Fig. 5A). At the transverse tarsal joint the navicular presents a broad, deeply concave depression in which the head of the astragalus rotates. The sustentacular facet covers the ventral surface of the neck and wraps around its medial side, blending with the navicular facet (Fig. 5A, lower). The posterior facet on both the astragalus and calcaneus is long, narrow, and angled slightly dorsolaterally (Fig. 6A, upper). The cuboid presents a smooth proximal projection against which the concave, arc-shaped cuboid facet of the calcaneus rotates. There is a slight, gently curved, volar enlargement on the plantar surface of the calcaneal tuberosity (Fig. 6A, lower).

Comparisons and contrasts with primate and nonprimate analogs

Sarmiento (1983) called attention to a process on the plantar surface of the calcaneal tuberosity (referred to above in *Varecia*) that serves as the origin for and increases

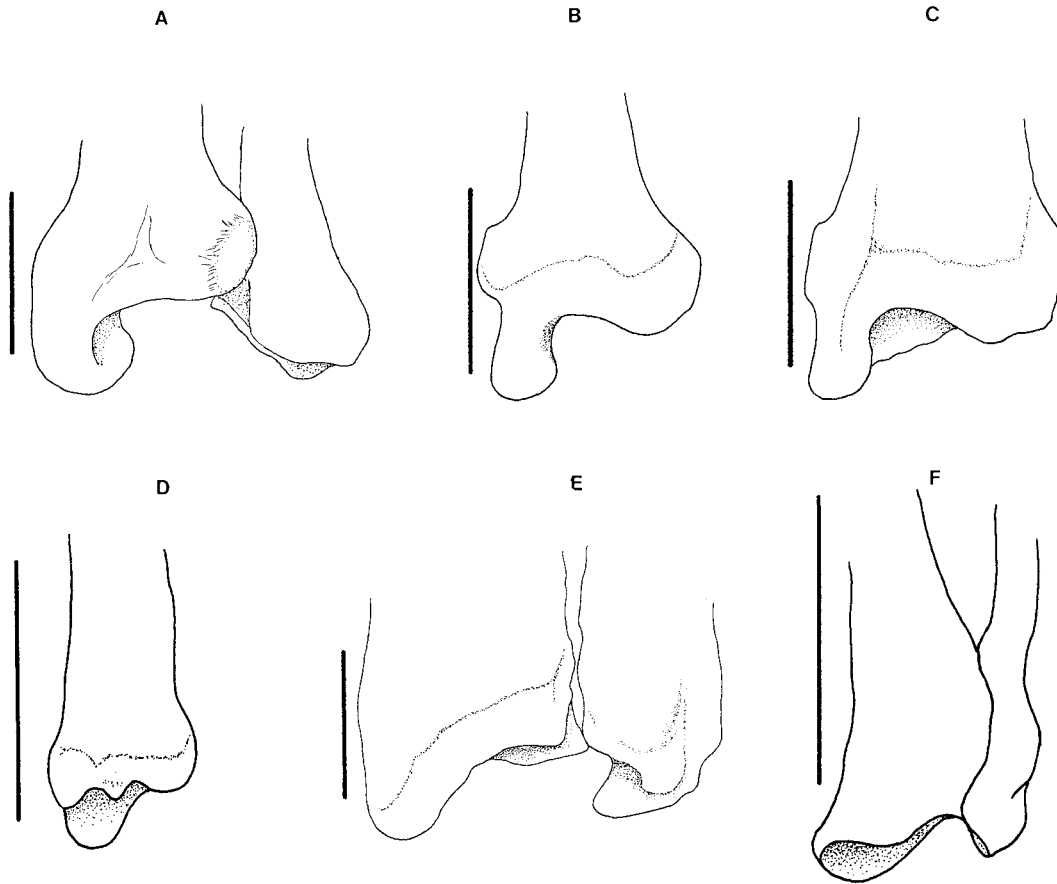


Fig. 4. Posterior view of left distal tibia and fibula of *Varecia* (A); left distal tibia of *Potos* (B), *Nasua* (C), and *Sciurus* (D); and left distal tibia and fibula of *Choloepus* (E) and *Cyclopes* (F). Scale bars, 1 cm.

the leverage of the superficial head of flexor digitorum brevis. He noted that the heel process and the calcaneal origin of the muscle are seen in primates that habitually hang from their hindlimbs, such as *Chiropotes*, *Ateles*, *Alouatta*, and *Pongo*. Sarmiento observed that during extreme plantar flexion when suspended by the hindlimbs, the long digital flexors are to the left of the muscle's length-tension curve and consequently are unable to produce maximal tension. In contrast, flexor digitorum brevis, from its calcaneal origin, is equally efficient in all positions of ankle plantarflexion. Furthermore, the expanded heel process increases its leverage. Thus, the digits can maintain a firm grasp even while the foot is fully plantar flexed.

Fleagle and Meldrum (1988) examined the tarsal morphology of *Chiropotes satanas* and described a combination of features they suggested were associated with suspension generally, including a separate tibia and fibula, a broad tibia suggesting that movement is not restricted primarily to the sagittal plane, a short medial malleolus that permits a great amount of ankle flexibility, and a small knob on the inner surface of the medial malleolus. Features of the tarsus in *Chiropotes* that are associated with hindlimb suspension include a spherical astragalar head with an expanded articular surface, an extensive articular surface for the calcaneocuboid joint, and a proximodistally short cuboid. *Chiropotes* has been observed in the wild to regularly adopt hindlimb suspensory

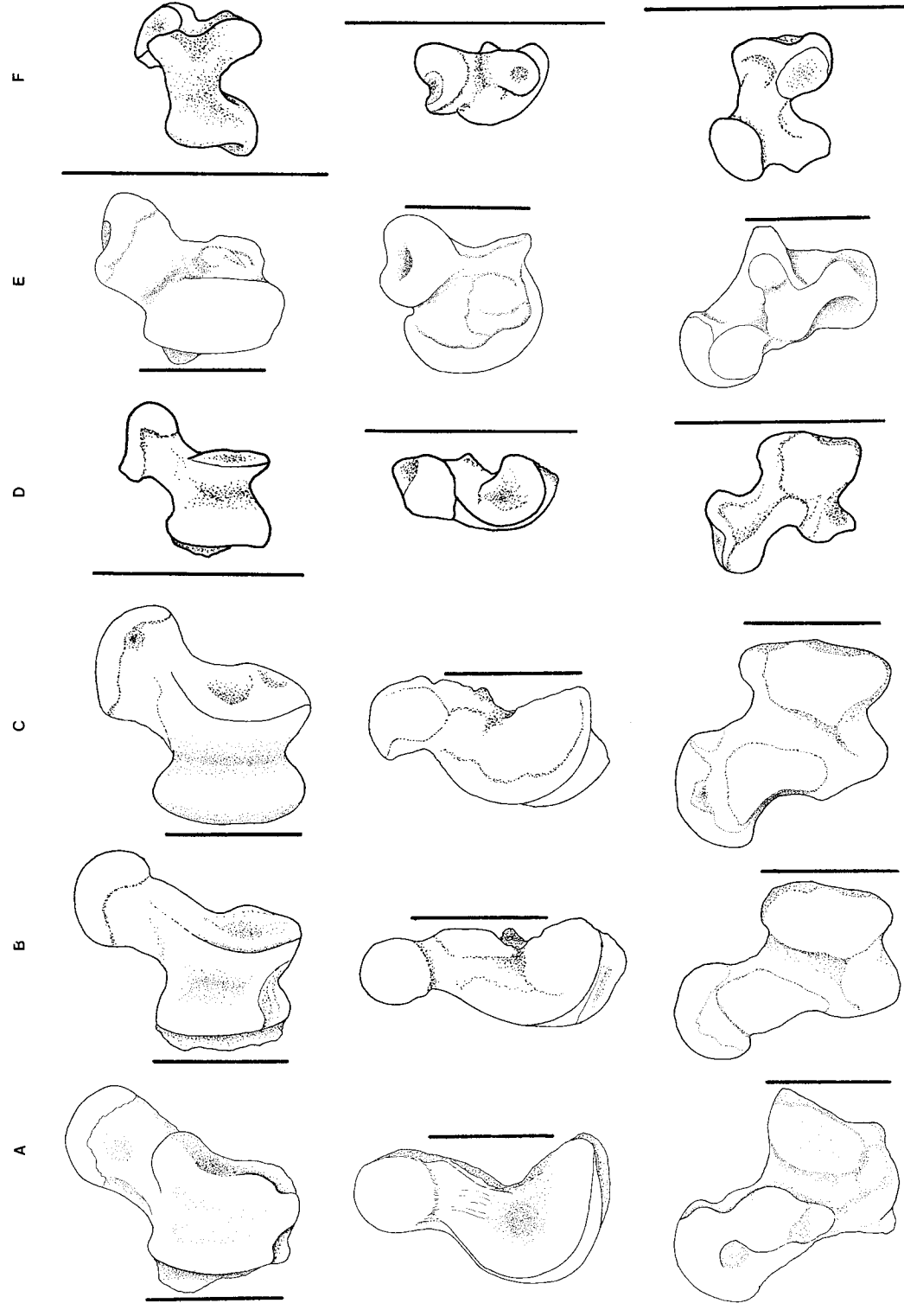


Fig. 5. Left astragali of Varecia (A), Potos (B), Nasua (C), Sciurus (D), Choloepus (E), and Cyclopes (F). Upper row, dorsal view; middle row, medial view; lower row, ventral view. Scale bars, 1 cm.

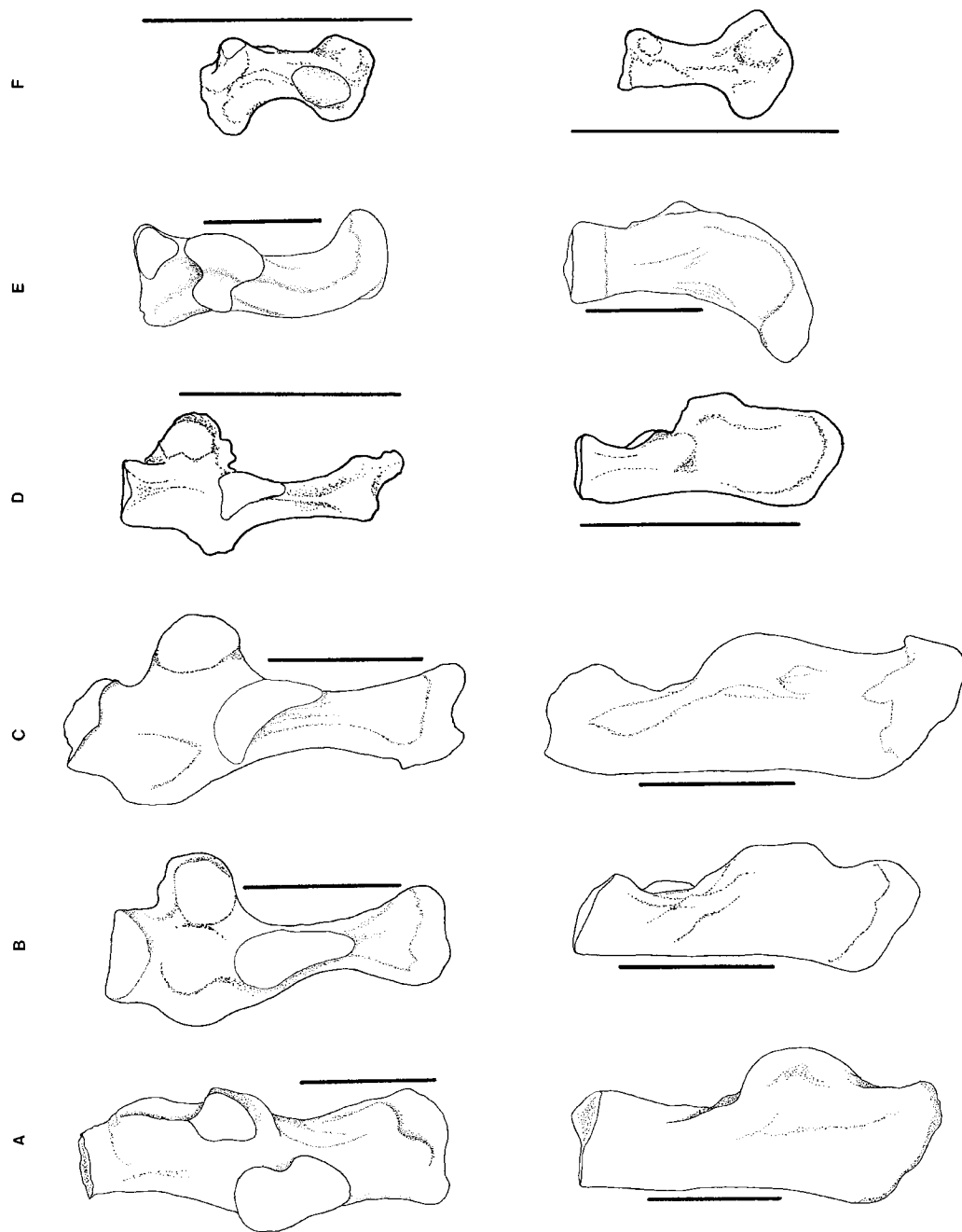


Fig. 6. Left calcanei of *Varecia* (A), *Potos* (B), *Nasua* (C), *Scotus* (D), *Choloepus* (E), and *Cyclopes* (F). Upper row, dorsal view; lower row, lateral view. Scale bars, 1 cm.

postures, although it is primarily quadrupedal (Walker, 1994).

Many of these skeletal correlates of hind-limb suspension are seen in other mammals that practice similar suspensory behaviors. Jenkins and McClearn (1984) provided a comprehensive description of the structure of the hind foot and movements allowed at the astragalocrural, subastragalar, and transverse tarsal joints in a variety of mammals that reverse the hind foot, including members of the orders Carnivora (*Potos*, *Nasua*, *Felis*) and Rodentia (*Sciurus*).

A number of similarities to the morphology exhibited by *Varecia* tarsals are noted and have been examined further in skeletal collections. For example, in the kinkajou's (*Potos flavus*) tibia and tarsus the medial malleolus of the tibia has a bulbous medial projection that rotates within a concave facet on the astragalus (Fig. 4B). The astragalar trochlea has a longer medial articular surface that is extended posteriorly and is hemispherical, spanning 180 degrees (Fig. 5B). Its asymmetry results in mediolateral rotation of the foot along its long axis in plantar and dorsiflexion. The astragalar head is spherical and widened mediolaterally, and the narrow neck is angled medially. On the calcaneus, the slightly concave sustentacular facet (Fig. 6B, top) receives the corresponding convex facet on the astragalus, which extends along the ventral and part of the medial surface of the astragalar neck (Fig. 5B, bottom). The medial extent of this facet reflects translation of the calcaneus during extreme inversion. The posterior calcaneal facet is long and convex and oriented in a manner that allows medial rotation of the calcaneus in inversion. The cuboid facet is crescent-shaped, which Jenkins and McClearn (1984) recognized as a feature that facilitates rotation between the cuboid and calcaneus. Sarmiento (1983) observed that small arboreal carnivores, including the kinkajou, seem to lack a heel process on the volar surface of the calcaneus. However, there is a bony expansion on the most distal volar aspect of the calcaneal tuberosity that is conspicuous, although not as prominent, as those described for *Ateles*, *Alouatta*, *Pongo*, or *Chiropotes* (Fig. 6B, bottom).

Nasua (the coati) is in the same family as the kinkajou. It is useful to compare the foot structure of the two genera because the coati is not as arboreal as the kinkajou. When in the trees they occasionally suspend from branches or descend tree trunks headfirst (McClearn, 1992). The hind foot is partially reversed in these positions, but the coati cannot achieve the extent of rotation at the pedal joints seen in the kinkajou. Jenkins and McClearn (1984) pointed out that the structure of the tarsal region is nevertheless highly similar in kinkajous and coatis. They note only two features that clearly distinguish the coati: the relatively reduced arc of curvature of the medial astragalar trochlea, and the wider posterior calcaneal facet (compare Figs. 5B and 5C). These features together serve to limit the coati's range of plantar flexion at the talocrural joint and inversion at the subtalar joint; in fact, Jenkins and McClearn (1984) noted that the hind foot of the coati has only half the potential range of movement of the kinkajou's hind foot. We make note of a few other features that distinguish the less mobile hind foot of the coati from that of the kinkajou. The medial malleolus lacks a pronounced medial knob (Fig. 4C), the fibular facet is flat instead of concave, the astragalar neck is wider and shorter (Fig. 5C, upper), the sustentacular facet is confined to only part of the ventral surface of the neck and does not wrap around its medial side (and therefore inhibits inversion) (Fig. 5C, bottom), the posterior calcaneal facet sits at less of an angle, and the plantar surface of the calcaneus is nearly flat (Fig. 6C, bottom).

The morphology of the ankle region in tree squirrels (*Sciurus variegatoides*) is very similar to that of kinkajous except for a few features. The tibial malleolus is short and lacks the bulbous projection into the medial side of the astragalus (Fig. 4D). Although the astragalar trochlear morphology is similar in the two species in being divided and extended posteriorly on the medial side with a 180 degree arc of curvature, there is a greater discrepancy between the two sides in squirrels (Fig. 5D). The medial trochlea has a very tight arc of curvature, while the lateral side is quite elevated and its articular surface extends anteriorly (Fig. 5D,

middle). The mediolaterally broad head of the astragalus has a small concavity on the ventral edge for a projection on the proximal facet of the navicular (Fig. 5D, bottom). The posterior calcaneal facet is relatively wide, and the cuboid facet is smooth and round, enhancing supination (Fig. 6D, top).

Features that tree squirrels hold in common with *Varecia* include an asymmetrically shaped astragalar trochlea with a longer medial side spanning 180 degrees, a medio-laterally broad and globular astragalar head, a medially angled astragalar neck (Fig. 5D, top), a long astragalar sustentacular facet that covers the ventral surface of the neck (Fig. 5D, bottom), a very long and convex posterior calcaneal facet (Fig. 6D, top), and a slight projection on the volar aspect of the tuberosity (Fig. 6D, bottom).

Felis wiedii, the margay, is a felid that suspends from its hind limbs and descends trees headfirst, with full reversal of the foot. The margay exhibits many features of the tarsal region correlated with this behavior that are more reminiscent of kinkajous and *Varecia*, as discussed above, than of other cats (Jenkins and McClearn, 1984). Other features of note include a medial malleolus that projects into the concave medial side of the trochlea and an oblique distal tibial articular surface. The medial side of the trochlea has a long, highly curved arc of curvature and is asymmetrically shaped; the lateral side is much higher than the medial. The cuboid facet is shaped like a wide arc and is concave; it rotates on the cuboid which manifests a slight convex projection on its ventromedial aspect. There is a very slight volar projection of the calcaneal tuberosity.

Examples of other suspensory eutherians with very different tarsal morphologies are *Coendou*, *Pteropus*, *Cyclopes*, and *Choloepus*. The Brazilian tree porcupine (*Coendou*) grasps with and hangs by its hind feet but it does not exhibit an overall pedal morphology like that of the taxa discussed so far. Some of its peculiar features include a large volar pad surrounding a "tibial ossicle" that facilitates grasping, a plantaris brevis muscle, an oblique axis of rotation at the talocrural joint, an extremely abbreviated medial malleolus, and a two-part navicular

that surrounds both the distal and medial aspects of the bulbous astragalar head (Wood Jones, 1953). The astragalar neck is very short, and the lateral side of the trochlea is longer than the medial, but it does not span 180 degrees. The posterior calcaneal facet is very wide and short, and there is no volar expansion on the calcaneal tuberosity.

The fruit bat, *Pteropus*, exhibits a convex knob on the ventral surface of the astragalus that pivots in a concavity on the calcaneus, facilitating axial rotation and reversal of the pes (Barnett, 1970).

Xenarthrans offer probably the strongest evidence that distinct morphologies can facilitate superficially similar behaviors (White, 1993; Meldrum et al., 1995). The tree sloths (*Bradypus* and *Choloepus*) and the pygmy anteater (*Cyclopes*) suspend from the hindlimbs, and only *Choloepus* descends headfirst. The combination of long, highly curved ungual phalanges, and the absence of a functional hallux (also characteristics of the porcupine *Coendou*) clearly distinguish both taxa from other hindlimb suspensory mammals.

The two-toed sloth *Choloepus* prefers to move among networks of lianas in large canopies (Mendel, 1985). Mendel (1981) observed that while feeding or exploring, *Choloepus* maintains contact with its hindlimbs more consistently than with its forelimbs. Grasping may be accomplished by flexing only the long ungual phalanges, which further increases the reach distance. Captive two-toed sloths have been known to fully hang by the hindlimbs alone, and they are able to reverse the hind foot 180 degrees at the ankle in this position (Mendel, 1985).

On the distal tibia, there is a single, narrow, hemispherical, concave facet for articulation with the astragalar trochlea. The medial malleolus is deeply grooved posteriorly for tibialis posterior, and it is widely separated from the medial side of the astragalus. The medial part of the distal fibular articular surface forms a facet for the trochlea that is continuous with the distal tibial facet; thus the trochlea is enveloped by the distal end of both bones. The distal fibula also bears a pointed, smooth, conical protuberance that projects medially into the deeply concave fibular facet of the astraga-

lus, forming a type of ball-and-socket joint (Fig. 4E). The astragalar trochlea is a single, narrow, highly convex surface with a very long arc of curvature (Fig. 5E). This arrangement permits an enormous amount of movement at the talocrural joint, including plantar and dorsiflexion, inversion, and adduction (Mendel, 1981). The foot can be plantar flexed until the dorsal aspect of the calcaneus contacts the posterior tibia and fibula. The neck of the astragalus is long, narrow, and angled medially (Fig. 5E, upper). The head is globular but not spherical like in other eutherians. There is a thick, convex rim on the medial and ventral aspects that meets the navicular and cuboid, but the dorsolateral aspect is a concavity that pivots on a convex navicular projection (Fig. 5E, upper and middle). The facet for the sustentaculum tali extends along the ventromedial surface of the neck and is continuous with both the navicular facet and the posterior facet (Fig. 5E, lower). The posterior facet is saddle-shaped and rectangular and it faces ventromedially, blending into the rough pit inside the concavity of the fibular facet, and this facet directs medial translation of the calcaneus in inversion, which has a similarly complex, saddle-shaped posterior facet (Fig. 6E, upper). The calcaneus presents a slightly concave, round facet for the cuboid, on which it pivots. A great amount of inversion (or supination) is permitted at the transverse tarsal joint (Mendel, 1981). One of the more striking features of the foot of *Choloepus* is the calcaneal tuberosity, which has an enormous volar expansion. The most volar and posterior aspect of the tuberosity is enlarged and angled slightly medially (Fig. 6E).

Choloepus manifests some muscular adaptations that further differentiate it from other hindlimb suspensory animals. The most striking modification is the conversion of tibialis anterior and extensor hallucis longus from dorsiflexors to plantar flexors of the pes; the tendons pass around the medial side of the pes to the volar surface to insert on the tendons of flexor digitorum longus, guided by the tuberosity. Soleus, another plantar flexor, passes around the calcaneal tuberosity and is continuous with quadratus plantae in some specimens (Mendel, 1981).

The flexor tendons are maintained within the tendon tunnel formed between the calcaneal tuberosity and the elongated medial cuneiform.

When the foot is extremely plantar flexed, as it typically is in *Choloepus*, the long flexors of the digits lose some power. Both flexor digitorum brevis and quadratus plantae, however, originate on the calcaneal tuberosity. Flexor digitorum brevis has two heads in *Choloepus*; the larger originates from the calcaneal tuberosity and inserts into the lateral two flexor tendons, while the smaller originates on the medial cuneiform and inserts with the medial tendon. The volarly and medially enlarged calcaneal tuberosity increases the leverage of flexor digitorum brevis and quadratus plantae as flexors of the pedal digits and invertors of the pes (Fig. 6E, lower).

The pygmy anteater, *Cyclopes*, is a fully arboreal, slow climber with a prehensile tail; it frequently suspends from the hindlimbs while reaching for food items (van Tyne, 1929; Crandall, 1964). It lacks a functional hallux; grasping with the foot occurs between the four digits and an enlarged heel pad (Wood Jones, 1953). The heel pad surrounds the calcaneal tuberosity and a greatly elongated tibial ossicle attached to the medial cuneiform and navicular (Fig. 7B); this morphology is just one of the many peculiar aspects of the pedal anatomy of *Cyclopes*. The distal tibia is extremely broad and anteroposteriorly compressed, with two small, widely separated facets for the sides of the astragalar trochlea. The medial malleolus is tiny and does not extend distal to or contact the trochlear surface (Fig. 4F). The trochlea of the astragalus is extremely wide and distinctly divided into a long, gently convex lateral surface and a small medial knob (Fig. 4F, upper; 4A). The lateral side of the trochlea slides in a deep groove created by the distal tibiofibular joint (Fig. 5F). The knoblike medial side acts as a pivot, allowing some mediolateral rotation of the tibia on the astragalus (Fig. 5F, middle). A wide range of plantar and dorsiflexion occurs at the talocrural joint; in fact, most of the articular surface of the lateral side of the trochlea actually faces posteriorly instead of dorsally (Fig. 5F, middle; 7C).

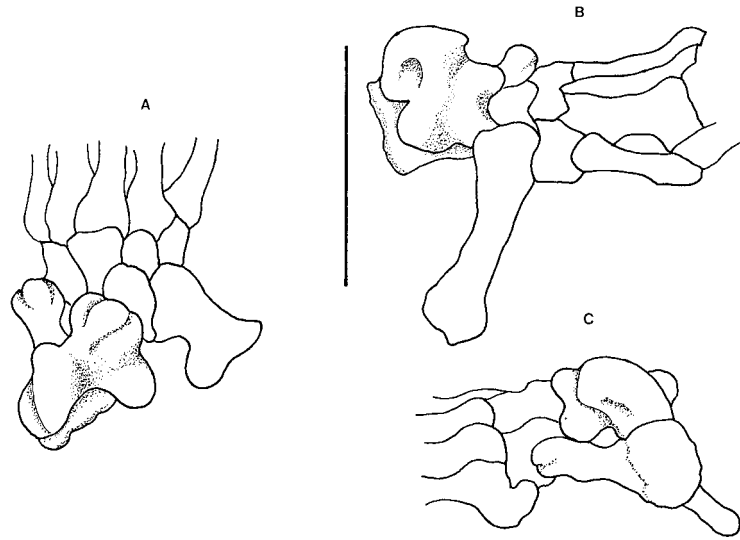


Fig. 7. Dorsal view (A), medial view (B), and lateral view (C) of the left proximal pes of the pygmy anteater *Cyclopes*; stippled bones are the astragalus and calcaneus. Scale bar, 1 cm.

The astragalar head is convex and bulbous on the ventromedial side, with a concave dimple for a pointed projection of the navicular on the dorsolateral rim on which the astragalus pivots. A small dorsal lip rotates around the conical projection and prevents hyper-dorsiflexion (Fig. 5F, middle; 7A,B). The astragalar neck is angled medially, but it is very short and wide (Fig. 5F).

The subastragalar joint morphology indicates that the astragalus can twist in a transverse plane on the calcaneus. On the ventral surface of the astragalus there is a convex articular surface that extends along the ventral surface of the neck and the medial side of the body of the bone, in two parts. Distally, it is continuous with the navicular facet. Laterally and posteriorly, there is a small, oval, slightly concave facet for the calcaneus. These medial and lateral facets are analogous to the facets for the sustentacular and posterior calcaneal facets, respectively, but they articulate with the calcaneus in a different arrangement (Fig. 5F, lower).

The calcaneus does not appear to have a developed sustentaculum tali; the anterior, ventral facet on the neck of the astragalus freely moves against a tiny facet on the distal aspect of the body of the calcaneus (Fig. 6F, upper). The posterior calcaneal facet is rounded and convex, and the astragalus can twist medially and laterally on this

facet on its posterior facet (Fig. 6F). The cuboid facet is hemispherically shaped and concave, and both mediolateral and dorso-ventral movement is permitted at the calcaneocuboid joint. The cuboid articulates between the distal calcaneus and the head of the astragalus in a triangular projection; the lateral side of the projection is convex, while the medial side is concave (Fig. 7A,C). There is a definite volar expansion to the calcaneal tuberosity, which functions as a support for the calcaneal heel pad along with the tibial ossicle (Fig. 6F, lower; 7C). *Cyclopes* has very well-developed pedal digital flexors and invertors of the pes, and also manifests a plantaris brevis muscle like *Coendou* (Wood Jones, 1953).

DISCUSSION

Grand (1972, 1984) noted an evolutionary trend among the primate radiations for increased "control of space" within the forest canopy, meaning the ability to efficiently and economically exploit the resources distributed throughout the three-dimensional space of the forest canopy. Particular attention was given the role of manual suspensory behavior in improving motion economy and increasing the feeding kinesphere. The greatest diversity of strategies is to be seen in animals of intermediate body size range (3–8 kg, including primates, rodents, and

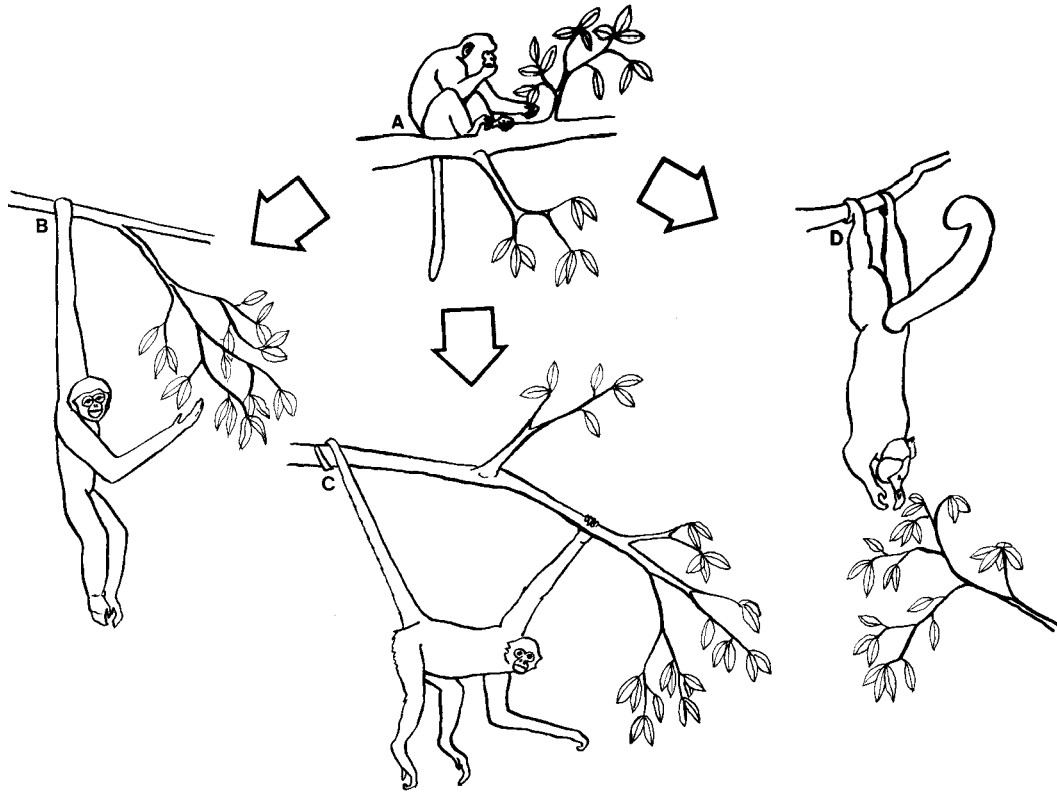


Fig. 8. Alternative strategies for exploiting feeding kinesphere in *Cercopithecus* (A), *Ateles* (B), *Hylobates* (C) and *Varecia* (D).

carnivores), especially in the exploitation of the terminal branch niche (Fig. 8).

Fleagle (1984) has suggested that primates with grossly similar dietary preferences occupying the same forest levels will avoid competition by employing different locomotor and postural strategies. The sympatric lemurids and indriids observed in Ranomafana National Park all occupy the higher levels of the canopy and exploit fruits to varying degrees. Each exhibits a somewhat distinct positional behavior repertoire: the *Eulemurs* are generally quadrupedal with limited or no hindlimb suspension, in contrast to *Varecia* and *Propithecus*, which are very suspensory, with *Propithecus* exhibiting additional differentiating specializations for clinging and leaping.

Other examples of niche partitioning via positional behavior differentiation are to be found among the anthropoid primates. For example, in the New World, the pitheciine

Chiropotes is sympatric with *Ateles*. They occupy the same canopy levels and exhibit a comparable degree of frugivory (Kinzey, personal communication). To some degree their niches are partitioned by their contrasting foraging strategies, one based on bimanual suspension assisted by a prehensile tail, the other by hind foot reversal and hindlimb suspension.

Hindlimb suspension is observed less frequently in cercopithecoid primates. One of us (DJM) has observed it under seminatural conditions in small captive cercopithecines. For example, *Cercopithecus cephus* was observed suspending bipedally from a small diameter horizontal support in order to reach suspended fruit (Fig. 9). An opposed grip was employed and the hindlimb joints were not as fully extended as was typically observed in *Varecia*. A greater reliance on the entwined tail was evident. It may be that the evolutionary history of the cercopithe-

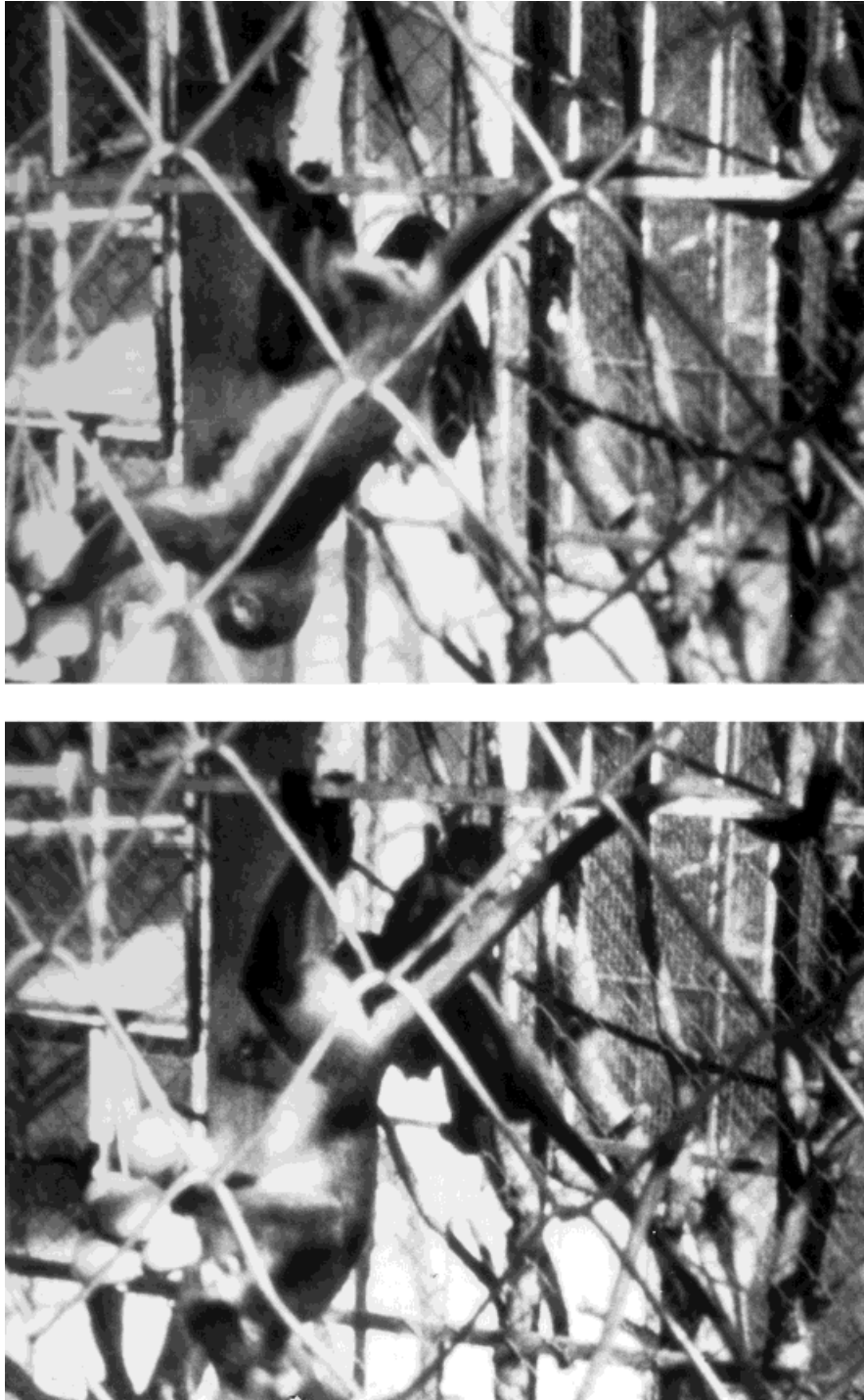


Fig. 9. Hindlimb suspension exhibited by a guenon (*Cercopithecus cephus*). Note the lack of full plantar flexion and the twining of the tail about the horizontal support (photo courtesy of June Rollinson).

coids has restricted their ability to exploit hind foot reversal during foraging. Adaptations for terrestrial locomotion have increased joint stability at the expense of mobility in the ankle of the the ancestral cercopithecoid lineage (Meldrum, 1991).

Another related primate positional behavior that has not been fully addressed in this paper is that of headfirst descent on vertical supports. Attention has recently been drawn to this behavior in the aye-aye (*Daubentonia*) by Curtis and Feistner (1994) and parallels were drawn with a number of primates (see also Tilden, 1990). Headfirst descent and postural suspension comprised a large percentage of positional behavior bouts in the aye-aye. The kinematics of foot reversal necessitated by headfirst descent are comparable to those employed in hind-foot suspension (Fig. 10). The presence of clawlike nails in *Daubentonia* and some smaller strepsirhines such as *Euoticus* and *Phaner*, as well as the callitrichines, further facilitates headfirst descent on large diameter vertical trunks, but such nails are not necessary for hindlimb suspensory postures.

Although the pedal morphology of *Varecia*, as a primate, is distinct in many respects from that of other mammals, it is clear that there is a suite of features of the tarsals that could be said to characterize some eutherians (i.e., primates, carnivores, and rodents) that reverse the hind foot. However, a similar end is achieved with very divergent morphological specializations in other types of suspensory eutherians. Noneutherians exhibit still other morphologies associated with these behaviors. The opossum, a marsupial, bears more than one facet on the astragalar trochlea; both mediolateral and anteroposterior movements occur at the astragalocrural joint (Jenkins and McClearn, 1984). Jenkins and Krause (1983) cited evidence for hind foot reversal in the multituberculate *Ptilodus*, in which abduction took place on two asymmetrical facets of the astragalocrural joint, while plantar flexion and inversion occurred at the subastragalar joint. (See also Krause and Jenkins, 1983.)

Each taxon exhibits some features that are peculiar to its own phylogenetic group. However, there are a number of features

that most or all of the taxa discussed here manifest; these common features may be mechanically required to enable the animal to adopt such extreme postures and to increase the range of movement at the astragalocrural, subastragalar, and transverse tarsal joints. All of the taxa discussed exhibit very long arcs of curvature on the astragalar trochlea; in all but *Coendou* the arc is greater than 180 degrees. The astragalar neck is angled medially in all the taxa, but it is not always elongated. The angle facilitates supination and inversion at the transverse tarsal joint. Although the sustentacular facet on the ventral surface of the astragalus varies in shape and position, it is generally expanded and extended along the ventral and/or medial side of the neck, and joined with the navicular facet; this arrangement increases the potential range of inversion. The posterior facet on the astragalus is smooth and concave, and does not inhibit movement at the subtalar joint. On the calcaneus, the facet on the sustentaculum tali faces primarily dorsally, with a slight lateral or distal tilt. The posterior calcaneal facet varies somewhat in shape and orientation, but it is generally smoothly convex and its long axis is angled. The cuboid facet is concave in all taxa, and though it may be either round or crescent-shaped, it permits rotation at the calcaneocuboid joint. Finally, the plantar surface of the calcaneus is not completely flat; there is some degree of volar expansion, which increases leverage of short pedal digital flexors.

There are some features that distinguish *Varecia* from the aforementioned nonprimate taxa. To what extent this is related either to its highly mobile hallux, the absence of the type of claws that characterize the rest of the taxa, or some aspect of its behavior, is unclear. In the rest of the taxa (except the sloth), the lateral side of the astragalar trochlea is higher than the medial; in *Varecia* the sides are nearly the same height, but the medial side is slightly higher. The fibular facet is saddle-shaped and it angles obliquely outward away from the astragalus. The most posterior aspect of the posterior facet of the calcaneus faces proximally, whereas it faces mostly dorsally in



Fig. 10. Hindlimb suspension exhibited by the aye-aye (*Daubentonia madagascariensis*). Note the lack of full plantarflexion in the upper ankle joint (photo courtesy of Duke Primate Center).

the other taxa. The form of the cuboid is unique, because it has a peglike proximal projection into the calcaneus around which axial rotation takes place.

While a suite of skeletal features can be defined that seems to characterize all of the hindlimb suspensory taxa in this sample, it

is clear that taxa with very divergent skeletal morphologies can perform superficially similar behaviors. Clearly hindlimb suspension is a significant foraging strategy that has arisen independently in a number of mammalian lineages. Particularly in the study of primate locomotion, this behavior

has not received due consideration as an alternative to manual suspension (Fig. 8).

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